

ACTIVE AND PASSIVE DISPERSAL OF LUMBRICID EARTHWORMS

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INTRODUCTION

Gates (1972), through the cooperation of the United States Bureau of Plant Quarantine, accumulated considerable evidence to support his hypothesis that the lumbricid fauna of northern North America represents principally species introduced there and distributed within the continent by man. Of the 3400 earthworm specimens seized by inspectors from imported plants during a 15-year period, nearly 1600 were lumbricids, representing 16 species. Because many of these species, in addition to other lumbricids, are holarctic or even "cosmopolitan" (*sic* Gates 1972) in distribution, it is easy to follow Gates' (1970, 1972, 1976a) reasoning that the present range of each reflects their transport to other regions by man. For North America, alone, Gates (1976b) lists 24 lumbricid species as "exotic," the source continent of most of these lumbricids presumably having been Europe; transport to North America was probably accidental, such as earthworms trapped in ship ballast or among the roots of imported plants.

In North America today, the dense distribution across the continent of many of these "exotic" lumbricids (*e.g.* *Lumbricus terrestris* L., *L. rubellus* Hoffmeister, *Aporrectodea* spp., *Octolasion* spp., and others) precludes the determination of the place(s) and time(s) of their introduction. Indeed, fossil evidence (Schwert 1979) indicates that at least one of these widespread "European exotics," *Dendrodrilus rubidus* (Savigny), was inhabiting North America over 10 000 years ago, certainly well before the arrival of European settlers. The limited distribution of some other "exotic" lumbricids in North America, however, clearly indicates the general region, if not the exact time, of their introduction to this continent. A population of the European lumbricid *Aporrectodea icterica* (Savigny), now well established in the region of an arboretum in southern Ontario, Canada, probably originated from trees imported to the site from England in 1971 (Schwert 1977). The limited distribution, outlined by Reynolds (1976) of *Lumbricus festivus* (Savigny) within the Saint Lawrence watershed of eastern North America, appears to represent a species introduced to

that region in one or more isolated localities decades or perhaps centuries ago and since slowly expanding its range outward from the valley.

Unfortunately, Gates and others have probably relied too much on man as the agent responsible for the present lumbricid distribution in northern North America. Certainly while being a major, if not the primary, influence on earthworm distribution, man cannot claim responsibility for the total distribution. We now know that endemic earthworms, including geophagous species, often densely inhabit the northern Appalachians and even some deglaciated areas of the continent; given so many thousands of years since deglaciation "to eat their way" (*sic* Gates 1976a) over these mountains, it is not surprising to find the endemic lumbricids *Bimastus* or *Eisenoides* throughout the state of Pennsylvania and even into New York and Massachusetts.

The seemingly sedentary nature of earthworms is misleading. In northern North America, most lumbricids are remarkably active throughout the spring and autumn, and, in the southern regions, winter. Whether one accepts or rejects Gates' premises on their present distribution, the wide and dense distribution of many of these species across North America have benefited from their extraordinary abilities at natural dispersal. Of the three to be mentioned, one is an active mechanism, while the other two involve passive dispersal through other natural agents. All three are in need of further investigation, and additional mechanisms probably exist.

STREAM DRIFT

The moist lowlands adjacent to streams and lakes are often ideal habitats for many species of Lumbricidae. Significant activity of these earthworms at or near the surface occurs when temperature, moisture, and light conditions permit. Inevitably, many individuals are washed into these waterways from surface runoff resulting from rainfall and snowmelt or from mass movements of soil during erosion, and they can potentially be transported long distances downstream. Bouché (1972) noted that several species of earthworms inhabit only particular drainage basins in France and hypothesized that stream drift was probably an important factor in influencing their distribution. Ward (1976) applied a similar hypothesis to explain the recolonization of a riffle area by the lumbricid *Eiseniella tetraedra* (Savigny) in a Colorado stream. Although adult lumbricids can remain submerged in aerated water for prolonged periods (Roots 1956; Edwards and Lofty 1972), the mortality rate of

individuals must be high during stream transport due to predation and physical battering. Nevertheless, live lumbricids can be frequently seen on stream bottoms, and the potential value of this drift to the dispersal of the species involved must be considerable.

During an analysis of a small stream in southern Ontario, Canada, Schwert and Dance (1979) recovered over 300 lumbricid cocoons from drift samples. Of the total, 92% were found to contain sperm and albumen or some stage in the development of the embryonic mass; these were believed, therefore, to be viable and potentially capable of hatching. From identification of the cocoons, they were found to represent at least six genera of Lumbricidae, all of them common to that region.

The small size and tough, spheroidal outer walls of these cocoons are, unlike the adult worms, ideally suited for long and rigorous transport downstream. Their palatability to fish is unknown, but presumably low. Roots (1956) demonstrated that cocoons, such as those of the lumbricid *Allolobophora chlorotica* (Savigny), could successfully hatch while submerged, with the young also undergoing normal growth in a submerged environment. From the remarkably high viability of the stream drift cocoons, their successful hatching could, likewise, be expected in areas of a stream where the cocoons had been deposited near the margin or in the bottom sediments of pools. Consequently, these transported species would become established in lowland areas downstream of their original source.

Since this study, numerous cocoons have been isolated from other streams in Canada and the United States, and this phenomenon appears to be widespread. Further investigation, however, will be needed to determine the degree in which such dispersal may have actually influenced lumbricid distribution.

MASS EMERGENCE

In northern North America and Europe, the mass emergence of lumbricids during periods of heavy rainfall or dew is a common, yet poorly studied, phenomenon. Such emergences were first described by Darwin (1881) and were subject to casual analysis by Friend (1924). Because this occurrence is more often witnessed in areas affected by human civilization, the deaths of often hundreds of thousands of individuals stranded on drying streets and sidewalks have led to popular conceptions that the dying earthworms were ill, poisoned, or drowned. Lankester (1921), Merker (1926, 1928),

Nishida (1951), and others, in search of a more scientific explanation, proposed that through chemotaxis the worms are forced to the surface as the oxygen supply to the soil is cut by rain saturation; Shiraishi's (1954) experiments failed to demonstrate this. Doeksen (1967) proposed that similar types of "migrations" observed in wet, foggy greenhouses result from behavioral changes in the worms resulting from increased hydrogen sulphide concentrations in the soil. Svendsen (1957), without seeking a chemical factor to explain surface activity, proposed that some species actively search for food sources during rain; in his experiments, he noted that several lumbricid species aggregated to dung through movements at or near the surface during moist conditions.

However precipitation actually triggers such surfacing, these mass emergences are so predictable in occurrence and so massive in scope, usually affecting several species at one time, that an additional hypothesis may be proposed with respect to the following two points:

1) Mass emergences occur primarily during periods of cool, moist weather. Friend (1924) noted emergences in England occurring only during the autumn, winter, and spring months. In North America, soil temperatures taken at a 3-cm depth during emergences in Ontario, Canada and in North Dakota, U.S.A. have ranged from 2° to 9° C. When soil temperatures rise above this range, as in the summer months, this phenomenon rarely occurs. A notable exception to this behavior is *L. terrestris*, which is known to surface for food and mating throughout the summer months.

2) Before human civilization, the original habitats of the Lumbricidae were primarily forests and forest meadows. Unfortunately, as previously noted, most observations of mass emergences have been in urbanized areas, where the earthworms are trapped by man-made structures and quickly killed by desiccation and sunlight. This surfacing phenomenon, however, also occurs on the forest floor, where the surfaced individuals are protected from desiccation, sunlight, and large predators by the tree canopy and by litter cover. During periods of cool litter temperature and sufficient moisture to permit respiration, the lumbricids may enter the litter and migrate through it rapidly and for long distances without the need to burrow. Contrary to popular belief, surfaced individuals can rapidly re-enter the soil in areas where it is sufficiently porous.

With this combination of proper soil temperature, sufficient moisture from fresh precipitation, protection from

sunlight and predators, and the loose litter medium for enhanced mobility, free and rapid surface dispersal can occur in relative safety. Such a behavioral response is advantageous to the species involved as it: 1) no longer limits the active outward dispersal of geophagous species to burrowing activity; 2) decreases population pressure during periods of peak reproduction and, therefore, food and space competition in areas of high earthworm density; 3) rapidly expands the range of the species involved; 4) enhances the possibility of genetic exchange among scattered populations of a species. The direction of dispersal movement appears to be random, even on sloping surfaces, and inevitably many individuals are washed into streams, potentially to colonize downstream areas.

In northeastern and northcentral North America, nearly all of the established species of *Lumbricus*, *Eisenia*, *Allolobophora*, *Octolasion*, *Aporrectodea*, *Dendrobaena*, and *Dendrodrilus* can be observed surfacing during proper conditions at cool times of the year. Several species of *Bimastos* are, likewise, known to surface. Sub-aquatic Lumbricidae inhabiting saturated environments, such as *Eisenoides lonnbergi* Michaelsen and *Eiseniella tetraedra* are, as would be predicted, unaffected by the precipitation trigger.

TRANSPORT BY OTHER ANIMALS

No published records apparently exist of earthworm individuals or their cocoons accidentally being transported by birds or mammals. Cocoons could be carried substantial distances if trapped in mud on birds' feet. Live individuals carried by predaceous birds are, from observation, occasionally dropped in midflight and could potentially reburrow. Certainly some of the intriguing earthworm records of James R. Philips (unpublished data, personal communication 1973 - 1975), such as immature *Lumbricus terrestris* apparently established in a kestrel (*Falco sparverius* L.) nest positioned on a tree limb 6 m above the forest floor, are attributable to avian transport. Whether such passive transport has profoundly affected earthworm distribution is impossible now to determine; in all probability, it has been of marginal significance.

SUMMARY

Although a number of lumbricid species now inhabiting North America were introduced there by man, human transport cannot alone account for their remarkably widespread establishment across the continent. Rather, many Lumbricidae are

capable of rapid dispersal through active or passive means other than by burrowing or by man. Dependent upon seasonal conditions, random movement of some species, often on a mass scale, occurs at or near the surface during periods of rainfall or of heavy dew; atmospheric and soil temperatures appear to be key factors in determining periods and size of such movements. Downslope dispersal of the Lumbricidae is facilitated by stream drift, especially during the cocoon stage in which up to 90% may remain viable after drifting often considerable distances. Avian transport of individuals is a small, but potentially significant mechanism of passive dispersal.

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QUESTIONS and COMMENTS

M.S. GHILAROV: The cause of emergence of earthworms on the surface is the deficiency of O₂ after heavy rains in summer in the soil. In spring after melting of snow earthworms don't emerge on the surface, whereas after spring flooding they don't die off, but after summer floodings of rivers they do perish. These facts were shown still in the 20's by Berclémisher and Chetyrkina. Certainly emergence on soil surface after summer rains allows the active dispersal and mixing of population; this has been stressed already e.g. by Perel and by Kvavadze.

Passive dispersal along slopes by rains is described by Atlavinyte, whereas in arid territories of Central Asia earthworms in natural conditions are known only along river benches (and subsequently along irrigation channels. So previous data of soviet zoologists are in accordance with your conclusions and support them.

A. TOMLIN: There are examples of L. terrestris rising and dispersing after rainfalls in July and August (3 cm soil temperature 12°C) though greatest emergence admittedly occurs April-June and Sept-Oct. I particularly refer to the Windsor Airport situation. I disagree that L. terrestris dispersal is limited to "cool" soil temperatures.

D.P. SCHWERT: Of all the peregrine species discussed, only Lumbricus terrestris regularly feeds on the surface. Surface feeding for this species does occur in mid-summer, when soil temperatures are greater than 9°C. I am surprised, however, at learning of a mid-summer mass phenomenon causing problems at Windsor.

A. CARTER: To what degree does the availability of areas for shelter affect the amount of earthworm movement after heavy rains? In flat grassy areas (city lawns), soil may become readily water-logged and earthworms have no hummocks for shelter.

D.P. SCHWERT: I have no quantitative information on which to answer this question. For reasons that I have just outlined, however, we could expect that the lack of shelter in such areas would lead to proportionally far greater mortality than in forests.

C.A. EDWARDS: You give the impression that the surfacing of earthworms after rain is confined to Lumbricidae in cool weather. It is common in hot weather in the tropics by Eudrilidae and Megascolecidae.

D.P. SCHWERT: I'm aware that other families do surface, however, I am not certain whether the same behavioral response for tropical earthworms is involved.

D. MALLOW: What studies, if any, have been done on rates of movement by lumbricid worms, with regards to their emergences during fall and spring rainfalls?

D.P. SCHWERT: At this time, I know of no such studies. My own research efforts in North Dakota are inhibited by low earthworm densities and limited rainfall in this part of the continent.